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AN EVALUATION OF PUTATIVE LAKE TROUT (Salvelinus Namaycush) SPAWNING SITES IN THE GREAT LAKES

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ABSTRACT

Approximately 827 lake trout spawning sites have been documented in the Laurentian Great Lakes generally decreasing in frequency with progression downstream. Offshore spawning sites were most common in Lake Michigan followed by Lakes Huron and Superior. Although spawning runs have been documented in six Canadian rivers in Lake Superior, none were reported elsewhere in the Great Lakes since 1897. Spawning was documented over all substrate types ranging from fine material (silt, clay and mud often associated with offshore and deeper sites) to bedrock; however, most were of coarse material (4 - 64mm) and the type varied among lakes (Lake Superior - angular rubble; Lake Michigan - pebble; Lake Huron - textured bedrock; Lake Ontario - cobble/pebble). Most spawning sites were between 0 - 20m with the most common depth in 0 - 10m in Lakes Michigan and Superior and 6 - 15m in Lake Huron. Spawning was reported at depths > 100m only in Lake Superior even though deep varieties of lake trout spawned in a wide range of depths in Lakes Huron and Michigan. While our observations all point to common characteristics for lake trout spawning sites (nearshore, < 10m in depth, coarse/clean materials), most sources were anecdotal. Direct evidence of spawning (eggs found, emerging fry caught or fish seen actively spawning) was available for only 31 (3.8%) of the reported lake trout spawning sites in the Great Lakes but still indicated similar characteristics of spawning sites.

RÉSUMÉ

Environ 827 frayères du touladi ont été identifiées dans les Grands Lacs. En général, leur nombre diminue progressivement de l'amont vers l'aval. Les frayères éloignées du littoral sont plus communes dans le lac Michigan, puis en ordre décroissant de fréquence, dans le lac Huron et le lac Supérieur. Même si des remontes ont été signalées dans six rivières canadiennes tributaires du lac Supérieur, aucune autre n'a été signalée dans les Grands Lacs depuis 1897. La fraie a été observée sur tous les types de substrats allant de matières fines (limon, argile et vase souvent présents dans les frayères éloignées du littoral et en eau profonde) à la roche mère; toutefois, la plupart des substrats étaient composés de matières grossières (4-64 mm) variant selon le lac (lac Supérieur - moêllons anguleux; lac Michigan - galets; lac Huron - substrat rocheux à grain; lac Ontario - galets/cailloux). La plupart des frayères étaient situées à des profondeurs variant de 0 à 20 m; dans les lacs Michigan et Supérieur, elles étaient plus fréquentes à des profondeurs de 0 à 10 m et dans le lac Huron, de 6 à 15 m. La fraie n'a été signalée à des profondeurs supérieures à 100 m que dans le lac Supérieur quoique des variétés de touladi des eaux profondes ont frayé à diverses profondeurs dans les lacs Huron et Michigan. Même si nos observations indiquent des caractéristiques communes des frayères du touladi (situées dans les eaux côtières, à moins de 10 m de profondeur, sur des substrats de matières grossières et propres), la plupart des sources de données sont anecdotiques. Des preuves directes de la fraie (présence d'oeufs, capture d'alevins nageants ou observations de géniteurs en action), n'étaient disponibles que dans le cas de 31 (3.8%) des frayères du touladi signalées dans les Grands Lacs, mais elles révélaient des caractéristiques semblables des frayères.

INTRODUCTION

The Laurentian Great Lakes once contained large numbers of fish stocks which supported commercial and sport fisheries (Hile 1946; Kaup 1978; Pycha 1972; Rahrer 1965; Rakestraw 1968; Smith 1892). However, native stocks of lake trout (Salvelinus namaycush) were severely depleted in much of Lake Superior and became virtually extinct in Lakes Michigan, Huron, Erie and Ontario during the 1940 - 50's (Baldwin et al. 1979; Christie 1972, 1973; Lawrie and Rahrer 1972; Pycha and King 1975; Smith 1968a; Swanson and Swedberg 1980; U.S. Department of the Interior 1969). Rehabilitation efforts directed at reestablishing self-sustaining lake trout stocks in the Great Lakes have met with partial success only in Lake Superior (Eshenroder et al. 1984). Although successful reproduction in residual native stocks in Lake Superior (Lawrie 1978; MacCallum and Selgeby 1987; Lawrie and MacCallum 1980) or elsewhere by introduced fish (Nester and Poe 1984), has been encouraging, restoration of lake trout stocks is far from complete (Henderson and Payne 1988; Hile et al. 1951a, b; King and Swanson 1975; Leach 1941; Pycha 1973). Eshenroder et al. (1984) indicated that reliance upon recruitment from stocks of hatchery origin will continue because rehabilitation efforts have not yet produced restored self-sustaining lake trout stocks.

The Great Lakes Fisheries Commission developed a series of seven goals for Lake Superior, to judge the success of rehabilitation measures. One of these goals was restored use of historical spawning reefs by lake trout (GLFC 1989). The goal of utilization of historical spawning sites by lake trout assumes an ability to identify these sites and/or an ability to identify characteristics of spawning locations. To determine common factors among spawning sites, we reviewed published material of lake trout spawning in the Great Lakes and 1) identified and enumerated spawning sites, 2)summarized depth and substrate characteristics, 3) evaluated information sources and summarized our state of knowledge for spawning sites in the Great Lakes.

METHODS

We conducted a literature review using Coberly and Horral (1980), Goodier (1981), Goodyear et al. (1982b-g) and Smith (1968b) as initial data sources. We collected references cited by the above authors by conducting a computerized literature search. We accepted each author's suggestion that a location was a spawning site and developed no criteria of our own for accepting/rejecting the author's assumption; thus, any biases are preserved. While our information search may not have been encyclopedic, our efforts were extensive and were sufficient to meet our objectives.

Any available information for location, depth, substrate type and original method of information collection was tabulated for lake trout spawning sites in the Great Lakes. Nomenclature of spawning sites was often confusing and, at times locations were unnamed. Therefore, we identified individual sites or an area of sites by number and used either the common name or left the site unnamed. [1]No attempt was made to supplement data for any site using alternate or additional sources such as hydrographic charts or bottom surveys etc. for any designated spawning site. Therefore, we retained any data deficiencies of the original published material.

Because authors used a variety of approaches to obtain data on spawning sites, we first categorized their method. Sites were identified using either direct or indirect evidence of spawning. Indirect evidence of spawning came from unknown and/or historical sources (historical government records, company fishing records, news clippings, and anecdotal sources), interviews with commercial fishermen, netting during spawning periods (netting during spawning periods was common particularly to secure reproductive products for hatcheries), or netting during any season

1. Tables from which summaries were constructed are available upon request from Great Lakes Lab. for Fisheries and Aquatic Sciences, Canal Drive, Ship Canal P.O., Sault Ste. Marie, Ontario P6A 1P0.

(information usually came from commercial fishermen and reference was often made to particular spawning locations). Direct evidence of spawning came from data provided by collections to develop methods and/or define egg deposition rates (centrifuge pumps, SCUBA divers, egg collection containers), collection of emergent fry (fry traps and occassionally fry/plankton nets), or direct observation of spawning in progress (by SCUBA divers, observers in boats or from shore).

We developed substrate size categories (from Nester and Poe 1987; Peck 1979) to accommodate verbal descriptions and the usual ranges for substrate measurements found in the literature. Two classes in our classification of substrate sizes (aggregate and granular) encompassed a larger range of particle size than the Wentworth categorization (Nester and Poe 1987). We also included verbal descriptions of site materials and believe we were able to adequately classify both the verbal descriptions and measurements of substrate type:

Bedrock:	Honeycombed or pitted limestone Dolomite Sandstone
Boulder:	> 256mm Rock of unknown size
Aggregate:	Cobble 64 - 256mm Pebble 4 - 64mm includes "rubble", "rock rubble" 4 - 256mm of Wentworth categorization
Granular:	Granular 2 - 4mm Sand 0.06 - 2mm includes "gravel"
Fine Material:	< 0.06mm Silt Clay Mud Moss

For depth of spawning, we relied solely on the information provided by the author and we summarized spawning site depths into 40 classes of 5 metre intervals. When spawning sites comprised a range in depths, we weighted depths accordingly (e.g. if spawning site depth was 2 - 9 m, entry in each of the 2 depth classes was weighted by 0.5).

RESULTS

We located 827 spawning sites in the Great Lakes (Fig. 1a - 1d). Approximately 96.3% of these were identified by indirect methods (Table 1). Conversely, direct evidence of spawning was used to identify only 31 sites (3.8%). We were unable to evaluate how 20.6% were determined to be spawning sites. The preponderance (71%) of spawning sites were identified from historical catch records or interviews (anecdotal sources) with fishermen. Although high capture rates of lake trout during spawning may not definitively indicate a spawning site, spawning likely occurs in that vicinity. These spawning sites were most often identified in Goodier (1981), Goodyear et al. (1982), Coberly and Horral (1980) and Smith (1968), all of whom extensively interviewed fishermen. Direct evidence was considered the most reliable information of spawning on spawning sites and was available for Lake Ontario (15% of identified spawning sites) followed by Lakes Michigan (6.3%), Superior (3.0%) and Huron (0.38%).

SPAWNING SITE LOCATION

Lake Superior

Two hundred and sixty-four spawning sites were identified near the shoreline of islands and the mainland of Lake Superior (Fig. 1a). Only 7 spawning sites (75, 164, 166, 168, 175, 235, 236) were found offshore and all were on/near hydrographically distinct shoals. The Apostle Islands area of Wisconsin (4 - 37) was an important spawning area (Dryer and King 1968; Kruegar et al. 1986; Peck 1975, 1977, 1979; Stanley 1987; Swanson 1973, 1976; Swanson and Swedberg 1980) and may have the greatest density of known spawning sites in the lake. Peck (1979) found numerous sites (40, 42, 53, 58, 61, 64, 65, 70, 73, 74, 79, 81, 85, 90, 93, 94,

101) along the southern shore of Lake Superior where lake trout catches were high during the spawning season and suggested that these sites had good potential for spawning. Michipicoten Island (159-163, 169, 170), Caribou Shoal (165), Superior Shoal (175) and Isle Royale (216-234) were all identified as major historic spawning sites (Pycha 1972; Rahrer 1965; Rakestraw 1968). With the exception of the Apostle and Isle Royale areas, most spawning sites were concentrated mid-way along the eastern and northern shore of the lake.

Loftus (1958), indicated that river spawning populations of lake trout occurred in the Montreal (132), Dog (151), Pukaskwa (157) and Eagle (152) Rivers. Spawning was also reported in the Michipicoten (149) and Steel (183) Rivers by Goodier (1981) who suggested that fish may enter other rivers but were unlikely to spawn there. Approximately 22 spawning sites (8.3% of total) have been documented in (6) or near (16%) rivers in Lake Superior. No spawning populations have been documented in U.S. rivers.

Hatchery and/or native lake trout have spawned (Jude et al. 1981; Peck 1984; Wagner 1981) on man-made deposits (artificial spawning sites) at the Presque Isle Harbour power plant water intake and discharge (88), Presque Reef (86), Cliff Dow Reef (87), the Munising Michigan Area (97a), Laughing Fish Point (90), Apostle Island (6-36), Keweenaw Bay Area (67) and Grand Marais Area (106).

Lake Michigan

Approximately 253 spawning sites were identified in Lake Michigan (Fig. 1b). The northern portion of Lake Michigan contains the greatest proportion (" 70%) of spawning sites. Approximately 1/3 of the spawning locations were found in the Green Bay (1-46) and Grand Traverse Bay (152-182) areas (Brown et al. 1981; Peck 1979; Wagner 1981). Spawning was also reported in many locations to the west of the Mackinaw Straits (183-217) and immediately south of Green Bay (48-72). Twenty-one deep (>35m) offshore spawning sites (77-84, 90-103) were reported (Coberly and Horral 1980; Harris and Eschmeyer 1975; Horral 1976; Norby and Collinson 1977), mainly in Wisconsin waters of the lake.

Wagner (1981, 1982) found lake trout egg deposition at several man-made structures, including Elmwood Marina (161), the Traverse City Municipal Power Plant (162) and Clinch Mountain Harbour (163). Other artificial spawning sites include the Kewaunee Power Plant (71), Point Beach Plant (72), Campbell Power Plant (118) and the Ludington Power Plant (118) (Brazo and Liston 1977; Chiotti 1973; Coberly and Horral 1980; Jude et al. 1981; Liston and Tack 1975). These artificial spawning sites were all in the northern half of Lake Michigan.

Spawning was reported in Kid's Creek and an unknown tributary in Traverse Bay area in 1847 and 1897 (Price and Kelly 1976; Ravenel 1898). While no spawning was reported in tributaries of Lake Michigan since the 1800's, 15 spawning sites near river mouths (28, 29, 33, 35, 38, 42, 63, 65, 73, 112, 118, 121, 126, 163, 170) have been documented (Becker 1976; Coberly and Horrall 1980; Organ et al 1978; Peck 1979).

Lake Huron

Two hundred and sixty-four spawning sites were identified in Lake Huron, Georgian Bay and the North Channel (Fig. 1c). Approximately 60% of the spawning sites were located near the islands and shoreline of the North Channel (75-171) and in Georgian Bay (172-201). Twenty-four spawning sites (21-46) were clustered on the western shore of the lake near Alpena, Michigan. Few spawning sites were found in the southern portion of Lake Huron. Only one (61) spawning site was reported south of the line joining Harbour Beach (Michigan) and Clarke Point (Ontario).

Few offshore spawning sites (29, 48, 49) were identified in Lake Huron. Six offshore spawning sites (160, 161, 162, 164, 165, 166) were found in Georgian Bay, and most were associated with shoals. Spawning in rivers was not documented; however, spawning adjacent to river mouths was common, particularly in Georgian Bay and the North Channel.

Lake Ontario

Forty spawning sites were reported on the Canadian shores of Lake Ontario and 2 were reported in U.S. waters (Fig. 1d). The majority (50%) of spawning sites were located on the northeast shore (2-9, 21-31) and others were reported in the Burlington/Toronto area (10-20). Spawning sites in the eastern end of Lake Ontario were all associated with the mainland and were generally near shore. Shoals in the Burlington (Ont.) area were apparently altered in 1830 - 1930, by construction projects, stone hooking and oil tar (Whillans 1979). In the western end of the lake, most spawning sites were near islands or shoals at the outlet of the lake.

Gannon et al. (1986) indicated that natural rocky reefs and shoals were infrequent in the nearshore of western Lake Ontario and compared the ecology of natural with artificial shoals. However, it was unclear whether spawning occurred at the man-made sites.

Lake Erie

Little information was available for Lake Erie (Fig. 1d). Five spawning sites were reported in Canadian waters, three in the western end of the lake and one on the northeast shore. We were unable to find any information on lake trout spawning sites in U.S. waters.

General

Spawning sites identified in the Great Lakes were most often along northern shores and were near the mainland, islands or distinct shoals. Several spawning populations were reported in Canadian rivers of Lake Superior and in two tributaries of Lake Michigan; none have been reported elsewhere. Spawning sites adjacent to river mouths were common and well documented, particularly in the upper Great Lakes. The frequency of reported spawning sites decreased with progression downstream in the Great Lakes (Table 1, Fig. 1). Offshore spawning sites were reported most often in Lake Michigan followed by Lakes Huron and Superior.

SUBSTRATE CHARACTERISTICS OF SPAWNING SITES

Although substrate at spawning sites are the product of geologic and glacial history, we aggregated spawning site substrates simply on the basis of material size. Our substrate classes were necessarily broad to allow us to incorporate studies with either direct measurements of particle size or verbal descriptions. However, classes broadly encompass the materials over which lake trout were reputed to spawn (Martin and Olver 1980;Scott and Crossman 1985; and others). When several authors studied the same site, we used their independent assessments of substrate size. As a consequence there may be additional bias in our summary and the number of descriptions of substrate type can exceed the number of spawning sites identified for each Great Lake.

While spawning site materials of glacial debris varied from site to site, sandstone aggregate was the dominant substrate type in Lake Superior (Fig. 2). Surprisingly, spawning was reported over each substrate type and fine materials (< 4 mm) occurred at 14% of sites with substrate information. However, coarser substrates (> 4 mm) were predominant and 77% of reported spawning sites with substrate information, occurred over boulder or aggregate type substrate. Of the aggregate class, cobble and/or rubble were common descriptions of spawning site materials.

In Lake Michigan, spawning sites were also found over each substrate type of dolomitic limestone base although 67% occurred over the aggregate class of materials (Fig. 2). Coarse (> 4 mm) substrates were again dominant, with 87.6% of spawning sites reported over these materials. Fine material occurred at 17% of spawning sites; however these data were largely from historic accounts (Smith 1909; Stockwell 1875) of lake trout spawning at greater depths (80-110 m) on clay.

In Lake Huron, spawning sites were reported to consist mostly of honeycombed

bedrock or aggregate materials and together comprise 77% of the reported substrate at spawning sites (Fig. 2). Bedrock was commonly reported to be deeply pitted and may or may not have been fragmented. Spawning site material was often described as angular in nature. Only 8% of lake trout spawning sites were reported to be on finer material (< 4 mm).

Although substrate was identified for only 9 lake trout spawning sites in Lake Ontario, almost half the sites were reported to be on aggregate materials (Fig. 2). Approximately 1/2 of the sites with substrate information were reported to contain finer materials along with aggregate material. Again, spawning sites were reported in all substrate classes although coarser materials predominated (56% of reported sites).

Aggregate materials (4-64 mm) comprised 54% of the spawning sites with substrate information in the Great Lakes and only 23% of sites were of fine material. Coarse materials predominated (86% of site descriptions) overall. Differences existed in substrate type among lakes as pitted limestone bedrock (honeycombed) was common in Lake Huron, while materials tended to be more rounded (cobble) in Lake Superior. Apparent differences in materials of lake trout spawning site likely result partly from differences in occurrence of the two major rock types in the Great Lakes basin (IJC 1977; Lawrie and Rahrer 1972; Stamm et al. 1980 a, b, c).

SPAWNING SITE DEPTH

Spawning sites were reported at depths from 15 cm to > 100 m (Fig. 3). Data for Lakes Erie and Ontario are not given as spawning depths were available for only a few sites. Our depth categorization will not define depth preferences of lake trout in other than broad ranges and only generally reflects differential spawning by depth. However, because most depths were estimated (> 75% of information came from indirect accounts of spawning) and few have related egg deposition to site depth, we feel our categorization is adequate for the lack of precision in the information available.

The majority of spawning sites (L. Superior 79.5%, L. Michigan 69.5%, L. Huron 83.5%) were at depths < 15 m and the modal class was either 0-5 or 6-10 m. In L. Superior, < 9.8% of sites were in water 125 to 185 m in depth. These sites appeared to form a distinct group where spawning occurred at considerable depth. A small group of sites (~2%) was also found at depths of 90-95 m in Lake Huron.

DISCUSSION

The brief, somewhat questionable spawning act (summarized by Martin and Olver 1980) may in part account for the diversity of spawning locations, substrate types, depths, time of year etc, observed in lakes throughout North America. Lake trout were reported to spawn in or at the mouth of a few rivers in Lake Superior, offshore shoals, around islands, along shores of the mainland and on all types of substrate from clay to bedrock at depths of 0.2 to 185m. The modal classes for substrate material and depth (Figs. 2 and 3) indicate that the majority of spawning lake trout select sites of 5 to 10 m in Lakes Huron and Michigan or 0 to 5 m (Lake Superior) over aggregate (Lakes Superior, Michigan and Ontario) and honeycombed bedrock (Lake Huron). However, the majority of historical spawning sites in the Great Lakes were identified by commercial fishermen, historic company and fishing records, and undocumented sources. The large variability in characteristics of spawning sites may therefore result from either plasticity by lake trout (of site selection) or inaccurate identification of spawning sites. We suspect that the diversity in site characteristics results partly from inaccurate identification of sites, but the possibility also exists that former stocks chose different sites (deep, offshore, fine materials).

Data collected from spawning sites using methods of direct egg and fry sampling (6% of identified spawning sites) indicate that spawning occurred in waters < 20 m (usually < 7 m), an exception being Eschmeyer (1955, 1956) who found 1 egg at 20 m and fry at greater

depths, and only over coarse material (Table 2). Although indirect sources indicate that spawning occured over all types of substrate material and to depths greater than 100 metres, the coincidence of direct and indirect sources of information indicate that lake trout currently appear to spawn only in shallow water over cleaned and coarse material (Table 3, Fig 3). If this is the case, then lake trout may select similar sites in inland as well as the Great Lakes.

It is difficult to find strong evidence supporting spawning at depths > 15 metres or over fine substrate material of < 4 mm diameter although Eschmeyer 1955 reports finding one egg at 20m, in Lake Superior. Since all eggs have otherwise been collected in waters of < 10 m, it may be reasonable to assume that spawning occurs only in shallow waters of the Great Lakes. Lakes other than the Great Lakes, reporting evidence of spawning, have recorded similar results at depths of < 10 m, with the exceptions of Caguga and Seneca Lakes in New York (Royce 1951; Webster et al. 1951) and Lake Nipigon (Dymond 1926). While evidence for deep spawning is not refutable, Sly and Widmer (1984) suggest that the deep spawning strategy of lake trout in Seneca Lake would currently be unsuccessful because of habitat conditions (temperature, organic/debris on substrate). Consequently, while we recognize that deep spawning may have occurred in certain stocks, current evidence points to the existence of shallow spawning sites.

Lake trout eggs usually filter through interstices in the substrate within hours or days after spawning and are provided with some degree of protection from predation (Martin and Olver 1980; Wagner 1981). We found that deep sites were generally comprised of fine materials which provided little or no protection. All data indicating deep spawning or spawning over fine materials originated from historical sources, therefore leaving us hard pressed to unequivocally accept that spawning occurred in these conditions.

Neither the substrate of spawning sites or the composition of lake trout stocks are immune to change. Bottom deposits may undergo modification from the physical forces induced by wind/wave action (Sly and Schneider 1984), by sedimentation (Sly and Widmer 1984) and by anthropogenic alteration (Hartmen 1972; Smith 1968b; Smith 1972; Whillians 1979). Therefore substrate characteristics identified historically may not exist today. Lake trout stocks have also undergone severe depletion resulting in extensive rehabilitation efforts largely through introductions (Eshenroder et al. 1984; Hile et al. 1951a; King and Swanson 1975; Leach et al. 1941; Pycha 1973) . The potential for change to spawning sites as well as altered stocks may therefore obviate the combination of historic data with current evaluations of spawning site characteristics. The possible inconsistencies between historic data with current conditions is emphasized by the current lack of evidence supporting spawning in rivers, as well as spawning in deep water over fine materials.

There is clear evidence from the Great Lakes that supports the general conclusions of Martin and Olver (1980) and Liimatainen et al. (1987) for lake trout spawning in inland lakes lake trout spawn in shallow (< 10 m (usually < 5 m), water over clean, coarse predominantly angular materials. While >800 spawning sites have been identified in the Great Lakes, only 31 sites were identified through the collection of reproductive products. Fourteen of these sites were man-made. The intention of restoring spawning at historical spawning sites incorporates a sound management philosophy. However, adequate screening of sites is required prior to significant expenditure of effort intended to develop spawning populations at candidate sites.

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Table 1: Summary of Source of Information and Evidence of Lake Trout Spawning in the Great Lakes.

	LAKE SUPERIOR	LAKE MICHIGAN	LAKE HURON	LAKE ONTARIO	LAKE ERIE
Total Number of Shoals	259	251	262	35	6
Number of Shoals Using Indirect Sources	203	174	192	13	6
Anecdotal	141	94	175	10	
Historical	75	82	28	10	1
Unknown	52	70	70	20	5
Netting	73	55	12	2	1
Predation of Eggs	8	4			
Number of Shoals Using Direct Sources	8	16	1	3	
Observed spawning	1	1		1	
Egg Deposits	4	12	1	4	
Emergent Fry	7	11	1	2	

Summary reflects multiple methods designation for single spawning sites.

Table 2: Summary Table of Direct Spawning in the Great Lakes

AUTHOR	# OF SAMPLED SITES	# OF ART.	# OF NAT.	RANGE OF SAMPLING AREA (m2)	RANGE OF DEPTHS (m)	SUBSTRATE	EGG COLLECTION PUMP	EGG COLLECTION PAIL	FRY COLLECTION PUMP	FRY COLLECTION TRAWL/SLED	FRY COLLECTION EMERGENT FRY TRAP	FRY COLLECTION MINNOW TRAPS	FRY COLLECTION PAILS	OBSERVED SPAWNING UNDERWATER CAMERA	OBSERVED SPAWNING GENERA
LAKE MICHIGAN	: 16 Individual sites														
Wagner 1982	4	2	2	15 to 55	2 to 15	Boulder, cobble, pebble & sand	4		2	2	3				
Dorr III et al 1981	1		1	11	3 to 12	Boulders to sand	1								
Wagner 1981	11	3	8		0 to 18	Boulders to sand	10			7	7				
Stauffer 1981	2	2			0 to 3	Boulders, rock rubble									
Jude et al 1981	1	1			3 to 15	Crushed limestone boulders & rock				1					
Rybicki and Keller 1976	1	(unknown # of sites)													
Stauffer 1979	3	3					6								
Wagner 1974	3		3	24.17	1.22 to 8.23	Boulder, gravel, rubble sand & bedrock	3				2				
Stauffer and Wagner 1976	6		6	465 to 1766	2.44 to 15.24	Rocky bottom with some sand & gravel	4		1	6					
Peck 1979	4		4												
Eshenroder 1988	1		1				4							1	
LAKE SUPERIOR	: 8 Individual sites														
Stauffer 1981	1	1			2 to 12	Rock Rubble to sand & mud	1	1		1	1	1			
Peck 1986	1	1		2833.5	2 to8	Pebble to boulders		1			1				
Peck 1984	1	1		450	~8	Pebble to boulders		1			1				
Peck 1981	1	1			2 to 12	Cobble and boulders				1	1	1			
Rybicki and Keller 1976	1	1				Rubble	1			1	1	1			
Stauffer 1979	2	1	1					1		2	2				1
Wagner 1974	1	1		5.6			1								
Eschmeyer 1955*	2	1	1		18.3 to 20	Rocky	1								
Eschmeyer 1956	5		5		96					1					
Wagner 1982	3	1	2		7.3 to 82.3					5					
Peck 1982	1	1			2 to 10	Cobble & small boulders		2		1	1		1		
Peck 1978	1	1			2 to 8					1					
								1		1					
LAKE HURON	: 1 Individual site														
Nester and Poe 1984	1		1		3 to 7	Broken cobble (30–60 cm)	1				1				
LAKE ONTARIO	: 3 Individual sites														
Sly and Schneider 1984	3		3		<1 to 7	Cobble, gravel, sand & silt	2								
Marsden et al. 1988	2		2		2 to 27	Gravel, cobble, course sand & pebble	1			1	2			1	

* One lake trout fry (age 0) and egg taken at 18.3m

Table 3: Comparison of Substrate Information from Direct and Indirect Evidence

	LAKE SUPERIOR		LAKE MICHIGAN		LAKE HURON		LAKE ONTARIO		LAKE ERIE	
	Direct Evidence	Other	Direct Evidence	Other	Direct Evidence	Other	Direct Evidence	Other	Direct Evidence	Other
Number of Shoals	8	250	16	235	1	261	5	30	0	6
Bedrock	1	19	2	66		130	1	3		
Boulders	5	36	11	71	1	51	2	1		
Aggregate	5	47	15	92	1	86	5	1		3
Granular		6	1	40		10	4	1		
Fine Material		12		27		7				
Depth (m)										
Egg Collection and Emergent	2 to 12		0 to 24.4		3 to 7		0 to 7			
Trawling	2 to 75						2 to 27			
Other		0 to 183		0 to 86		0 to 91		4 to 5		5.5 to 7.

Figure 1a Spawning Sites for Lake Trout identified in Lake Superior and their proximate location.

Figure 1b Spawning Sites for Lake Trout identified in Lake Michigan and their proximate locations.

Figure 1c Spawning Sites for Lake Trout identified in Lake Huron, Georgian Bay and North Channel and their proximate locatio[illegible].

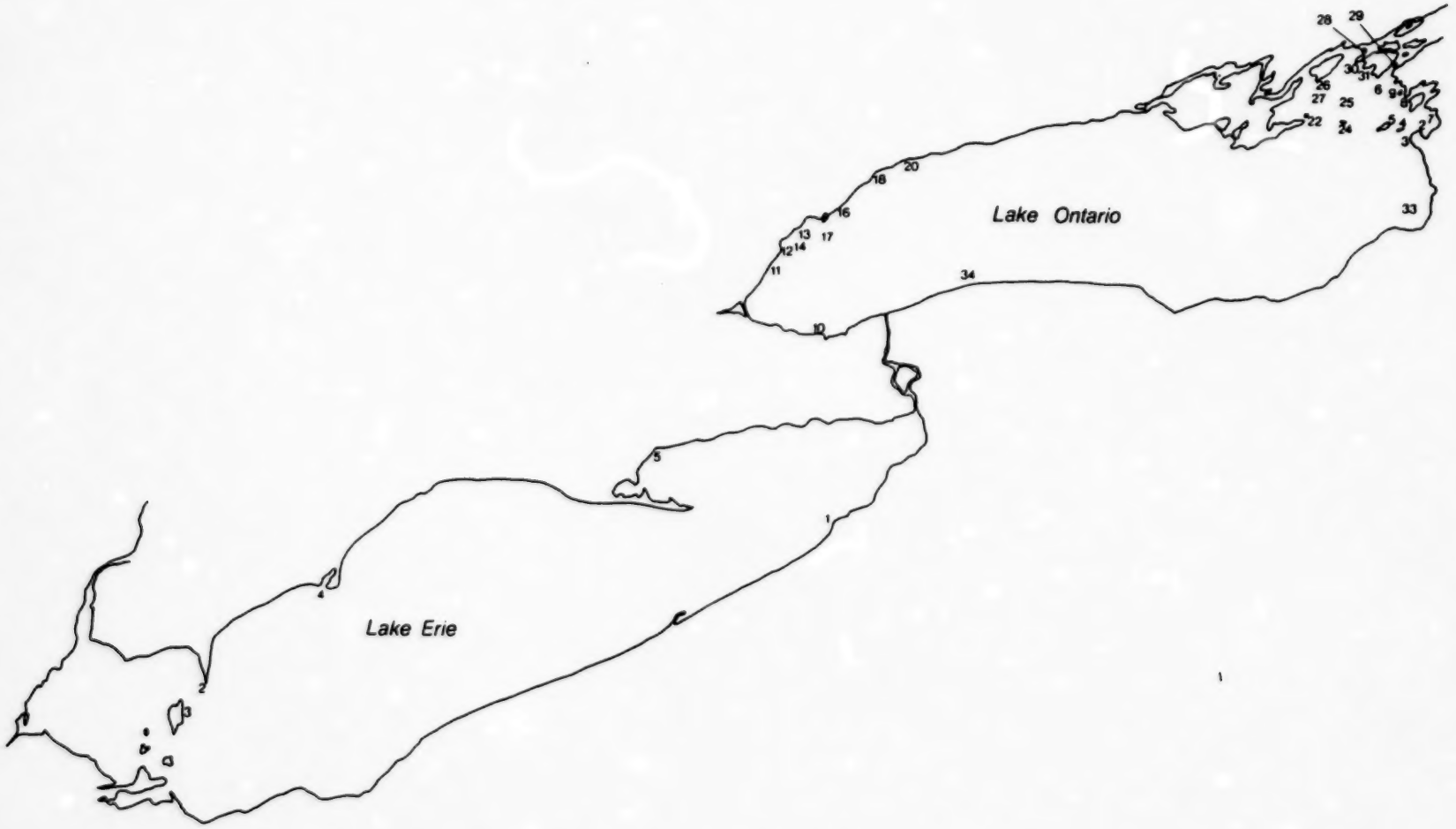

Figure 1d Spawning Sites for Lake Trout identified in Lake Erie and Lake Ontario and their proximate locations.

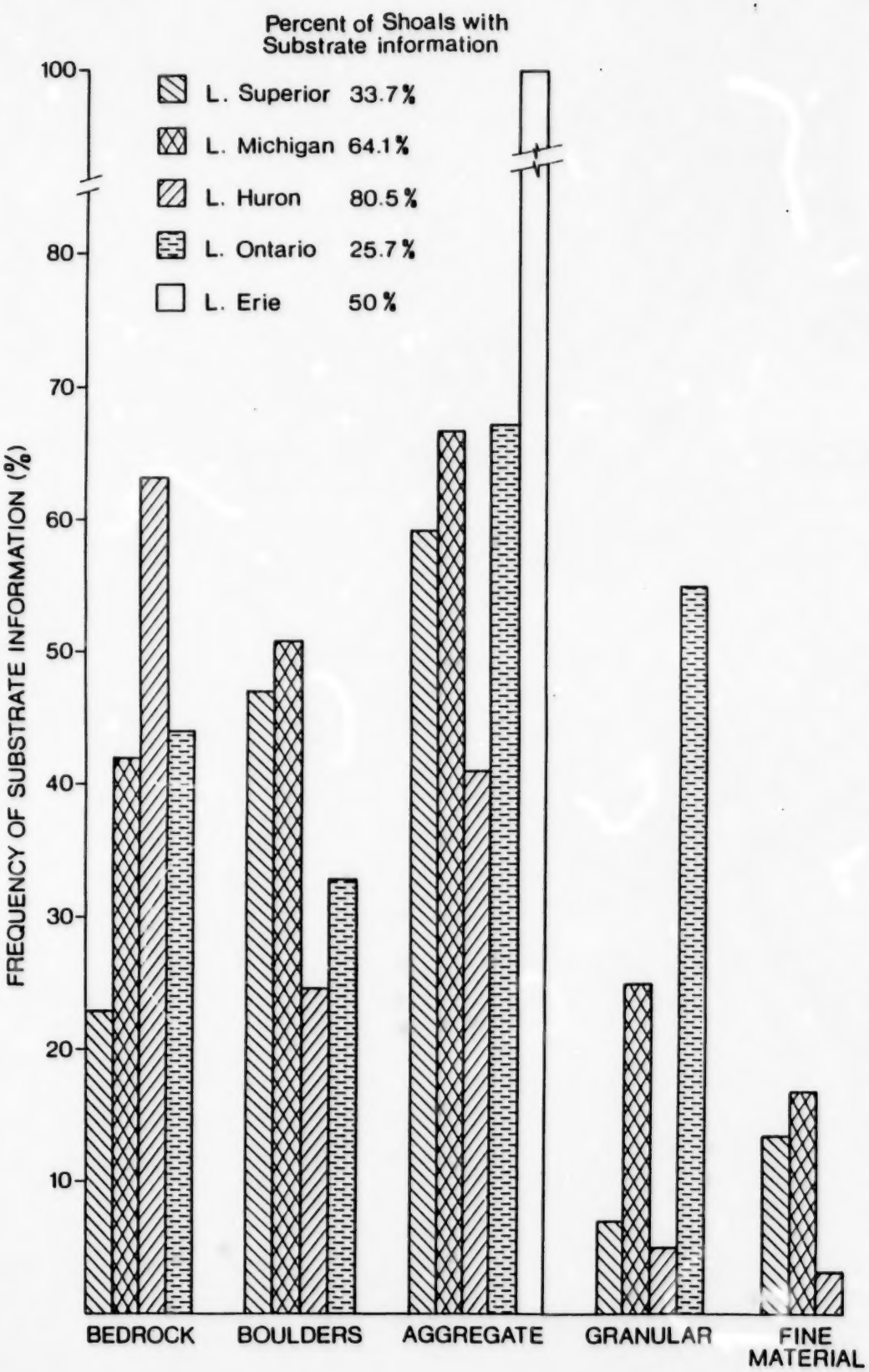
Percent of Shoals with Substrate information
L. Superior 33.7%
L. Michigan 64.1%
L. Huron 80.5%
L. Ontario 25.7%
L. Erie 50%
FREQUENCY OF SUBSTRATE INFORMATION (%)
100
80
70
60
50
40
30
20
10
BEDROCK
BOULDERS
AGGREGATE
GRANULAR
FINE MATERIAL

Figure 2.

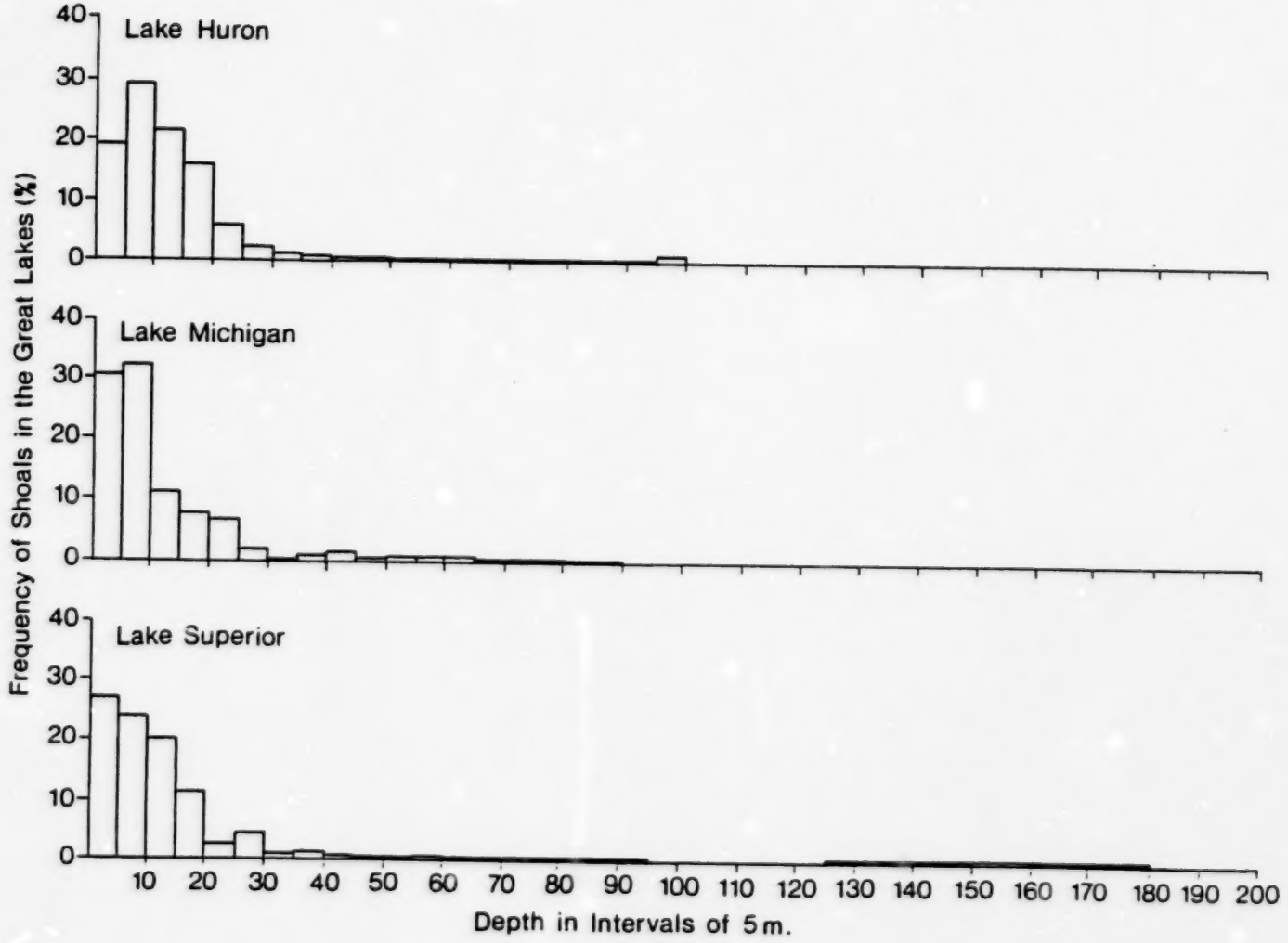
Lake Huron
Lake Michigan
Lake Superior
Frequency of Shoals in the Great Lakes (%)
0
10
20
30
40
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200
Depth in Intervals of 5 m.

Figure 3.